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A Morphological Study of some members of the Genus Pallavicinia

BY

DOUGLAS HOUGHTON CAMPBELL
PROFESSOR OF BOTANY

AND

FLORENCE WILLIAMS

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WITH TWENTY-THREE FIGURES

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CONTENTS

INTRODUCTION

The Liverworts, probably the most primitive of existing land-plants, offer many important morphological problems to the botanist. Among the Liverworts, no group is more interesting than that known usually as the Anacrogynous Jungermanniales, or, as less commonly denominated, the Metzgeriaceae.

While a good deal of work has been done upon the morphology of these plants, notably the important investigations of Leitgeb [1] and Goebel [1, 2] as well as the earlier studies of Hofmeister [1] and others, the minute study of their structure and development has been confined to a comparatively small number of species; and further investigations on

some of the less known forms must be done before it will be possible to determine the relationships of the different genera of the Anacrogynae.

At present the classification of the Anacrogynae is in a most unsatisfactory condition, and it is certain that radical changes must be made in the scope of certain genera, and in the grouping of the families as they are at present constituted.

Most of the Anacrogynae are plants of relatively simple structure, being thallose forms for the most part, although in certain genera, *e. g.*, Blasia, Fossombronia, Treubia, leaf-like marginal lobes are present; and the transition from the typically thallose Anacrogynae to the much more numerous leafy liverworts (Jungermanniales acrogynae) is by no means an abrupt one.

During a stay in Western Java, in 1906, a number of rare liverworts were collected, including several species of Pallavicinia. Among these were three which have been seldom collected, and which so far as we know have never been critically examined as to their anatomy and development. As it was thought that a careful study of these species might be of value for a better understanding of the morphology of the genus, the specimens were given to Miss Williams for investigation. The making of the preparations upon which the present paper is based, as well as most of the drawings, are the work of Miss Williams.

The genus Pallavicinia as understood by Schiffner [1], comprises the two old genera, Mörkia and Blyttia, of Gottsche. In his recent excellent résumé of the Liverworts, Cavers [2] has expressed the opinion that these older genera should be revived, and the name Pallavicinia be discarded. Should this view be accepted, all of the species here considerd would be transferred to the genus Blyttia, unless the sub-genus Mittenia is separated as a distinct genus.

Most of the species of Pallavicinia are found in the moist tropics, being especially abundant in the more elevated regions. Several species, however, *e. g., P. Lyellii,* occur in the more humid parts of the temperate zones.

Stephani, in his review of the Hepaticae [1], recognizes 29 species of Pallavicinia, which are placed in two sections: Procumbentes,[1] with 20 species, and Dendroideae,[2] with 9. In the Procumbentes (Eupallavicinia) the plant is a prostrate thallus (Fig. 1, *B*), usually attached for its whole length to the substratum by numerous rhizoids. The members of the section Mittenia have the thallus differentiated into two parts, a prostrate rhizome-like

[1]The section procumbentes = Schiffner's sub-genus Eupallavicinia.

[2]The Dendroideae = Mittenia Gottsch.

region, nearly or quite destitute of a lamina, and upright branches which grow from the rhizome. In these upright shoots, the lamina is broadly expanded and repeatedly forked. These dichotomously branched shoots resemble very closely the leaves of certain small ferns, especially the Hymenophyllaceae (Fig. 1, *A*).

Of the three species to be discussed in the present paper, two, *P. radiculosa* and *P. Levieri*, belong to the section Eupallavicinia, the third, *P. Zollingeri*, to Mittenia.

The general structure of the thallus is much the same in all species. Except for the rhizome-like portion occurring in some species, the thallus is differentiated into a very distinct midrib, several cells thick, and a delicate lamina, or wing, on each side of the midrib, these marginal wings being always in Eupallavicinia but a single cell in thickness; but in Mittenia they merge more or less gradually into the midrib. The midrib is traversed throughout its extent by a strand of conducting tissue composed of cells which are narrowed and greatly elongated, pointed at the ends, and with thick pitted walls.

Branching is of two types. In the first there is an apparent dichotomy, the equal branches having their midribs and conducting tissues continuous with those of the main shoot. The second type of branching has the appearance, superficially, of exogenous adventitious branches occurring on the ventral surface of the midrib. In these ventral shoots, the conducting tissue is not connected with the midrib of the main shoot (Fig. 2, *A*, *B*).

Rhizoids occur more or less abundantly on the lower surface of the thallus where it is in contact with the substratum.

All of the species are dioecious, the reproductive organs being borne upon the dorsal surface of the thallus. The antheridia, which are protected by scales, occur either upon the midrib or close to it. The archegonia are in definite groups which are surrounded by a double envelope, the outer one forming the "involucre," the inner envelope a more or less tubular sheath, the "perianth."

METHODS

Most of the material was killed with a 1% aqueous solution of chromic acid. Other material was fixed with alcohol containing 10% acetic acid. Larger specimens were also preserved in commercial alcohol. The material was imbedded in paraffin, cut uniformly 6μ in thickness, cleared in xylol, and stained variously for the study of different structures. Bismarck-brown proved the best stain for the vegetative parts of the thallus, except the conducting tissue, which was well differentiated by gentian-violet. The latter stain was also found useful in the study of the spermatozoids. These were not satisfactorily stained with either safranine or methyl violet. Haidenhain's iron-alum-haematoxylin proved much the best stain for the nuclei, and was well differentiated by either Bismarck-brown or Delafield's haematoxylin.

Pallavicinia (Mittenia) Zollingeri (Gottsh.) Schiffner.

Pallavicinia Zollingeri is one of the most striking members of the genus, and has hitherto been collected only from Java and Sumatra. The specimens here described were collected near the summit of Mt. Pangerango, an extinct volcanic cone in Western Java, nearly 10,000 feet in height. In this region the plant is very abundant, especially on the low banks along the trail, where it occurs in dense mats of considerable size. It fruits abundantly, and no trouble was experienced in securing an abundant supply of material in various stages of development. In May, 1913, the plant was found on Mt. Banajao, near Manila; and probably the same species was also found in the Benguet mountains. So far as we know, this is the first record of its occurrence outside Java and Sumatra. It grew at a height of about 2,000 metres, under much the same conditions as on Pangerango in Java.

From the slender, creeping rhizome the delicate fan-shaped erect shoots, which are about 6 cm. in height, arise, vivid green in color, and, as we have already stated, resembling so closely a delicate fern that they might very well be mistaken for it (Figs. 1, 5).

The method of growth is sympodial, the apex of the prostrate main axis turning upward, and developing into the expanded, leaf-like erect shoot. From the ventral side of the shoot, near the base, a branch develops which grows horizontally for a time, as a rhizome, and finally turns upward to form another upright frond.

The growth of the shoot is due to the activity of a single large apical cell (Fig. 3, *A*, *B*). This appears broadly triangular in section, with seg-

ments cut off from two of its surfaces. Sections through young shoots whose apices are just turning upward, showed in one case five apical cells, of which it was impossible to say which was the original one. Some of the initial cells had not yet divided, while in others one or more segments had been cut off. The original apex continues its growth upward, while these secondary initial cells are left behind, but later they may give rise to ventral shoots.

Fig. 1.

A. Male plant of *Pallavicinia* (*Mittenia*) *Zollingeri*. x 2.
B. Sterile plant of *P. radiculosa*, natural size; *r*, ventral branch.

One of these secondary apical cells begins active growth and gives rise to the shoot which continues the sympodium. It grows horizontally for a time, but finally turns upward and develops into the next upright green frond. Several segments are cut off from the apical cell before a differentiation of the different tissues of the shoot is apparent. Finally the midrib and lateral wings can be distinguished, and in the former the central strand of elongated cells appears. Thus, at the base of the shoot,

the conducting tissue is absent, and there is no connection between it and that of the older shoot from which the branch has arisen (Fig. 2, *B*).

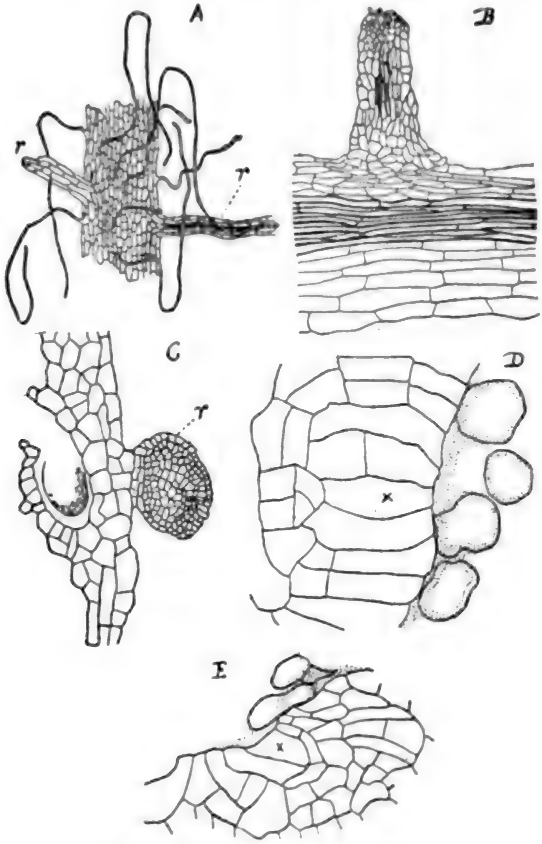

Fig. 2. *Pallavicinia Zollingeri.*

A. Part of the basal region of a frond, showing rhizoids, and two ventral branches, *r*.
B. Median longitudinal section of the base of a shoot passing through a young ventral branch. The conducting tissue of the main shoot and the branch are not continuous.
C. A ventral shoot (*r*) growing from the surface of the frond of an antheridial plant. The remains of an antheridium may be seen upon the dorsal surface.
D. The apical region of the shoot shown in *C*. *x*, the apical cell.
E. Apical region of a ventral shoot.

The other initial cells may never develop beyond cutting off a small number of segments. These groups of cells may be recognized for a long time on the surface of the shoot, near its base. Sometimes, however, one or more of these cell-groups resume activity, and from them

arise the slender, apparently adventitious branches which are often met with upon the ventral side of the shoots. These slender cylindrical root-like branches may be only a few cells in thickness, and are traversed by a conspicuous strand of conducting tissue, which can easily be traced to the base of the shoot, where it ends abruptly, and does not join the corresponding strand of the main axis. The occurrence of ventral branches is confined mainly to the prostrate portion of a shoot, or to the base of the stalk of the frond. They may, however, occasionally arise from the ventral side of the expanded portion of a frond, and in the only case observed (Fig. 2, *G*) the shoot was much broader than those arising from the stalk of the frond or from the prostrate rhizome. The frond from which this shoot arose bore empty antheridia.

The apical cell of *P. decipiens*, a species from Ceylon, strongly resembling *P. Zollingeri* in general appearance, has been carefully studied

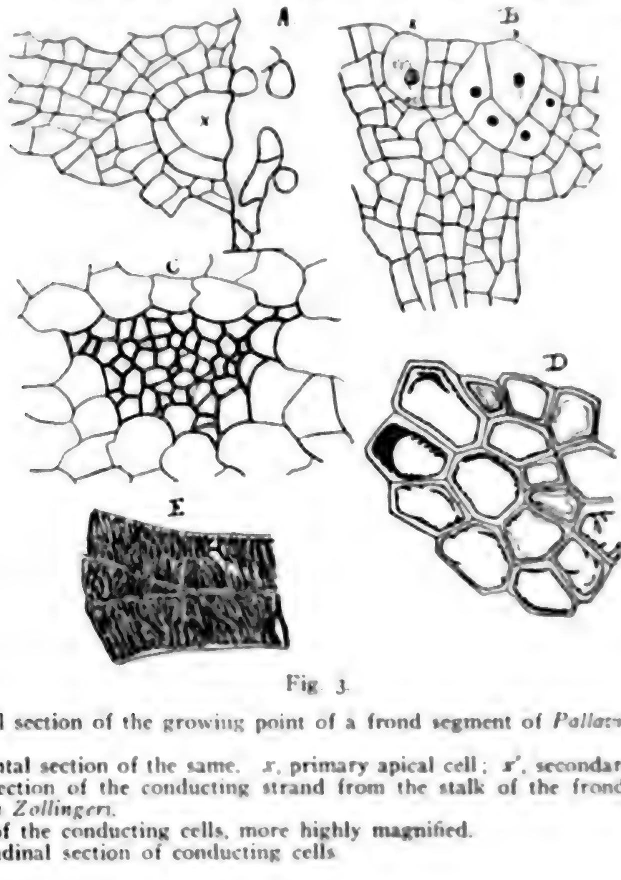

Fig. 3.

A. Vertical section of the growing point of a frond segment of *Pallavicinia Zollingeri*.
B. Horizontal section of the same. *x*, primary apical cell; *x'*, secondary apical cell.
C. Cross-section of the conducting strand from the stalk of the frond of *Pallavicinia Zollingeri*.
D. Some of the conducting cells, more highly magnified.
E. Longitudinal section of conducting cells.

by Farmer [1]. In this species the form of the apical cell is quite different from that of *P. Zollingeri*. It has the form of a three-sided prism. Four sets of segments are formed, three lateral and one basal, instead of the two sets of lateral segments found in *P. Zollingeri*.

Long, slender, simple rhizoids which are developed from the superficial cells, are formed in great numbers upon the prostrate rhizomes. Here and there occur isolated scales, one cell in thickness, and very much like those which cover the antheridia.

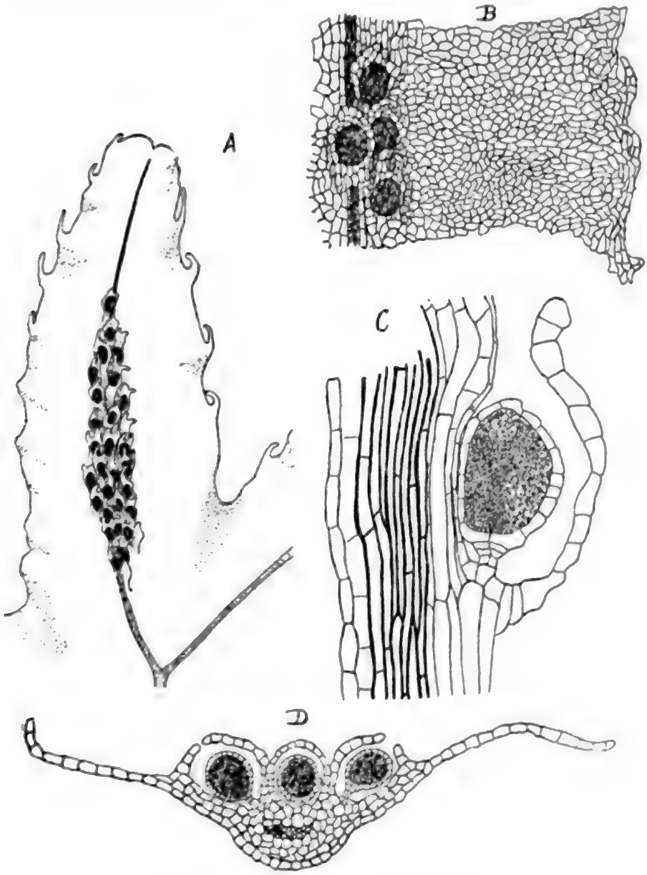

Fig. 4. *Pallavicinia Zollingeri.*

A. Segment of the frond of an antheridial plant, x 25 (about).
B. A portion of *A*, more highly magnified.
C. Longitudinal section of the shoot, passing through an antheridium, and showing the strand of conducting tissue.
D. Cross-section of a segment of the frond, showing the position of the antheridia on the dorsal surface of the midrib.

The cells of the ventral part of the midrib have thick walls in which are pits elongated transversely. These pits are in lines extending round the cell, and forming partial spirals, this being perhaps due to the longitudinal growth of the cell (Fig. 3, *D*, *E*). These cells, which are presumably conducting cells, have very little protoplasmic contents, thus agreeing with Tansley's description of the corresponding tissue in other members of the genus [1]. The cells of the cortical tissue of the rhizome contain many starch granules, in this respect recalling Cavers' figures of *Mörkia flotowiana* [2].

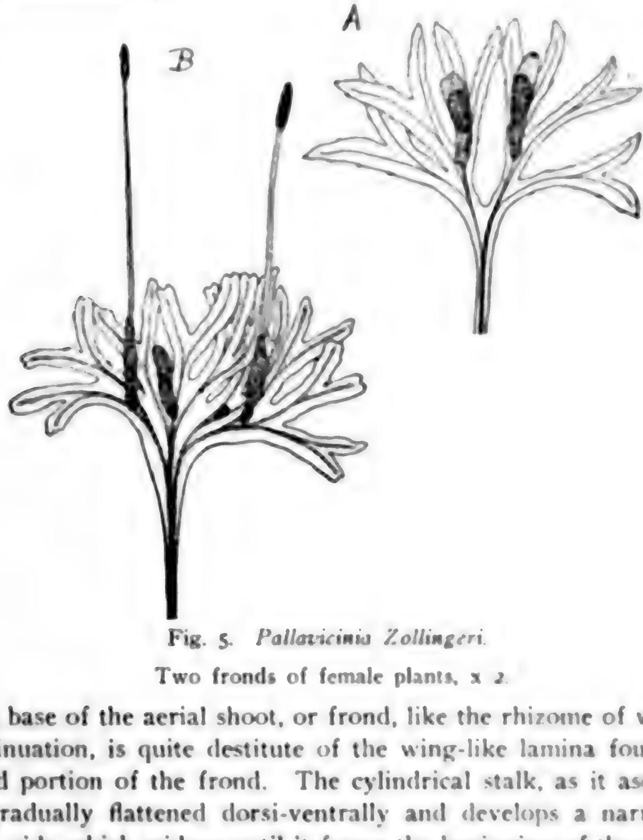

Fig. 5. *Pallavicinia Zollingeri.*

Two fronds of female plants, x 2.

The base of the aerial shoot, or frond, like the rhizome of which it is the continuation, is quite destitute of the wing-like lamina found in the expanded portion of the frond. The cylindrical stalk, as it ascends, becomes gradually flattened dorsi-ventrally and develops a narrow wing on either side which widens until it forms the beginning of the expanded, fan-shaped lamina of the frond. The first dichotomy occurs when the young frond is 3-4 cm. in height. The forking is repeated from two to four times, and there thus results the palmately divided leaf-like shoot, the slender central strands of the delicate segments simulating almost exactly the venation of a true leaf. In the archegonial plants these fan-shaped

fronds are about 2.5 cm. in width (Fig. 5). In the male plants they are somewhat smaller. The apex of each segment is indented, and the margin is wavy, with conspicuous teeth, or narrow lobes, which are usually pointed and hooked (Fig. 4, *A*).

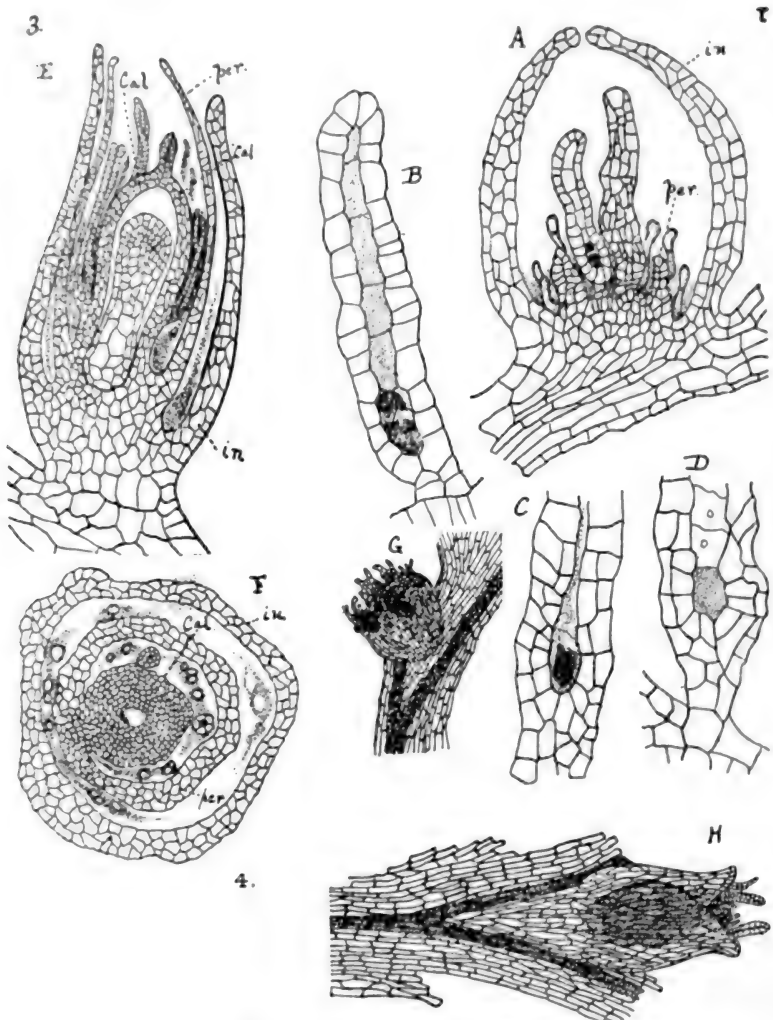

Fig. 6. *Pallavicinia Zollingeri.*

A. Median section of an archegonial receptacle; *in*, involucre; *per*, perianth.
B. A nearly mature archegonium.
C, *D*. Ventral part of two old archegonia.
E. Receptacle containing an embryo; cal. calyptra.
F. Transverse section of a similar receptacle.
G, *H*. Archegonial receptacles.

The male plant (Fig. 1, *A*) is smaller and more delicate than the female, while the lamina is more strongly corrugated. The antheridia occur in thick patches upon the dorsal surface of the midrib of the ultimate segments of the frond, and each antheridium is subtended by a scale whose margins may be either entire or toothed (Fig. 4, *A*, *B*). More than one crop of antheridia may be formed on a frond, and one sometimes finds old patches of scales with the remains of discharged antheridia on the older portion of the frond whose terminal segments bear younger antheridia. Fig. 4, *D* shows a cross-section of a segment of the frond, passing through a group of antheridia upon its dorsal surface. Fig. 4, *C* shows a longitudinal section of a frond-segment, passing through a nearly ripe antheridium, covered by its subtending scale.

The archegonial receptacles (Fig. 6, *G*, *H*) arise very close to the point where two segments of the frond diverge, and not infrequently actually at the fork, although not as a marginal structure. As the receptacle grows it overlaps the fork; but careful examination shows that it does not arise from the margin, but from a point some distance from it between two of the costae. Several archegonial receptacles may occur on a single frond, and always near the base of the lamina. Receptacles of quite different ages occur in close proximity, so apparently the development is not necessarily acropetal. The material was too old to show the young archegonia, and for the present the question as to the exact origin of the young receptacle must remain in doubt.

Pallavicinia radiculosa (Sande) Schiffner

Pallavicinia radiculosa is the largest species of the genus, and a most striking liverwort. The specimens used in these investigations were collected at Tjipanas, some remarkable hot springs on Mt. Pangerango, at an elevation of 2140 metres. The plants grow in large loose mats where the warm water oozes out of the mountain side. Tjipanas is the original locality for the species, and it has been collected at this place by a number of botanists. Schiffner states [2] that it is also known from Borneo, and Stephani [1] gives also a station in the Island of Mergui in the Bay of Bengal. It was collected in January, 1913, by Professor Campbell near Taiping in the Federated Malay States, growing upon a dripping bank, under much the same conditions as in Java, except that the location was only a few hundred feet above sea level instead of at an elevation of 2000 metres. The difference is to be explained by the fact that in Java the necessary heat was furnished by the hot springs about which it was growing. It is highly probable that further search will show the plant to occur in other parts of the Malayan region.

The plant has an elongated prostrate thallus with a thick and very conspicuous midrib (Figs. 7, *A*, 8, *E*). The thallus may reach a length of upwards of 20 cm. with a width of 7 mm. The thallus is usually forked and is attenuated posteriorly, due to the gradual suppression of the lamina. The midrib itself is practically of equal diameter throughout, and projects strongly on the ventral side. As already stated, the wings of the thallus become gradually narrower toward the base of the

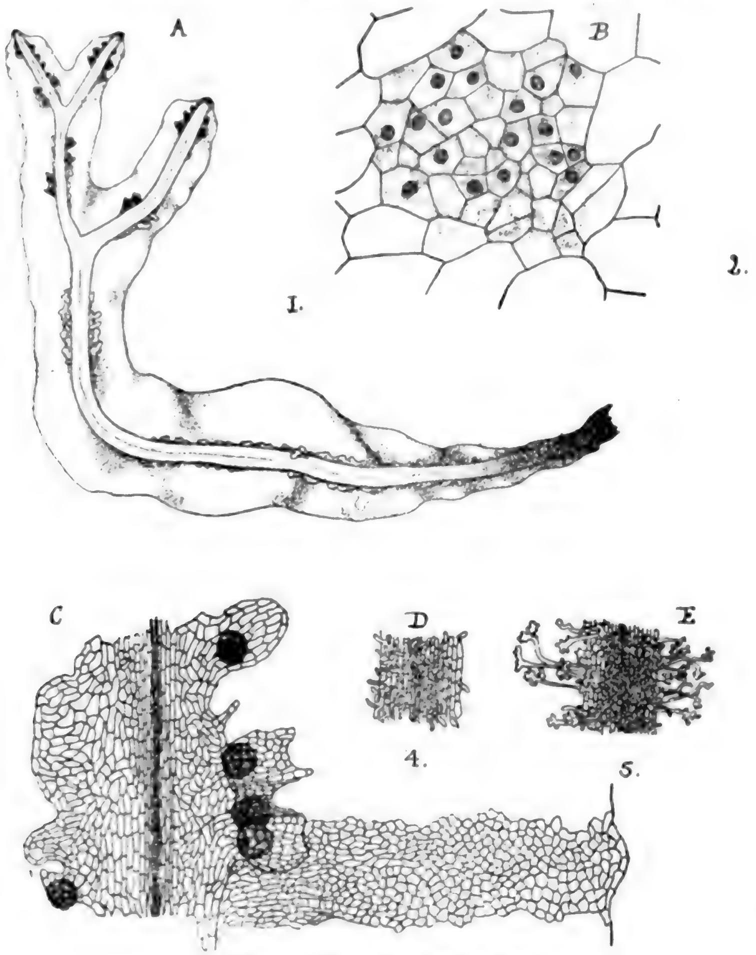

Fig. 7. *Pallavicina radiculosa.*

A. Male plant, x 3.
B. Cross-section of young conducting tissue, very highly magnified.
C. Midrib of the thallus, showing the position of the antheridia.
D. Young; *E*, older rhizoids.

shoot, and finally almost completely disappear, so that the oldest part of the shoot is almost perfectly cylindrical. The surface of the wings is smooth and the margin undulate, but not developing lobes or teeth, in this respect differing from *P. Zollingeri*.

The ventral surface of the midrib is completely covered by short papillate hairs, like the true rhizoids, outgrowths of single superficial cells. These papillae become longer in the older parts of the thallus, and gradually give place to the long, dark purple-red rhizoids, which in the basal region form a dense mass. These conspicuous rhizoids (Fig. 7, *D, E*) are composed of a single cell, but develop a number of short branches at the apex. As in *P. Zollingeri* ventral, apparently adventitious branches are developed which much resemble the main shoots, but are somewhat smaller. It is highly propable, however, that under favorable circumstances these develop into perfectly normal plants. Their origin was not investigated, but it is probable that they arise in much the same way as the similar branches in *P. Zollingeri*.

Quite frequently the wings of the thallus are attenuated anteriorly as well as posteriorly, and as a result the apex of the shoot is somewhat pointed. In form and size the male and female plants are very similar.

The antheridia form a row on each side of the midrib, and are arranged in elongated groups separated by sterile areas (Fig. 7, *A*). They are attached to the side of the midrib and project laterally, but are directed slightly forward. They are covered by broad scales, one cell in thickness, which arise at intervals behind an antheridium and, passing above it, extend along the side of the midrib as a shelf-like projection. These scales are deeply incised, scalloped, and sometimes toothed, varying much in size and shape. The scales may subtend a single antheridium or a small group. Sometimes no antheridium is formed under a scale (Fig. 7, *C*). The antheridia arise in strictly acropetal succession, and the scales near the apex cover immature antheridia only.

The female plants (Fig. 8, *E*) closely resemble the males, except for the different appearance of the reproductive organs. The archegonial receptacles resemble those of *P. Zollingeri*, but are much larger. They arise at various points upon the dorsal surface of the midrib, but there is no connection between their formation and the branching of the thallus. They possess the conspicuous perianth and involucre characteristic of the other members of the genus. The archegonia are much more numerous than in either of the other species examined. The involucre, also, is more conspicuous, having a deeply incised spreading margin, which is strongly revolute.

The growing point of the shoot lies at the bottom of a more or less evident notch, formed by the active growth of the tissue on each side of the apical cell. The latter has segments cut off only from its two lateral faces. Seen in horizontal section (Fig. 8, *C*) it is a narrow triangle, with

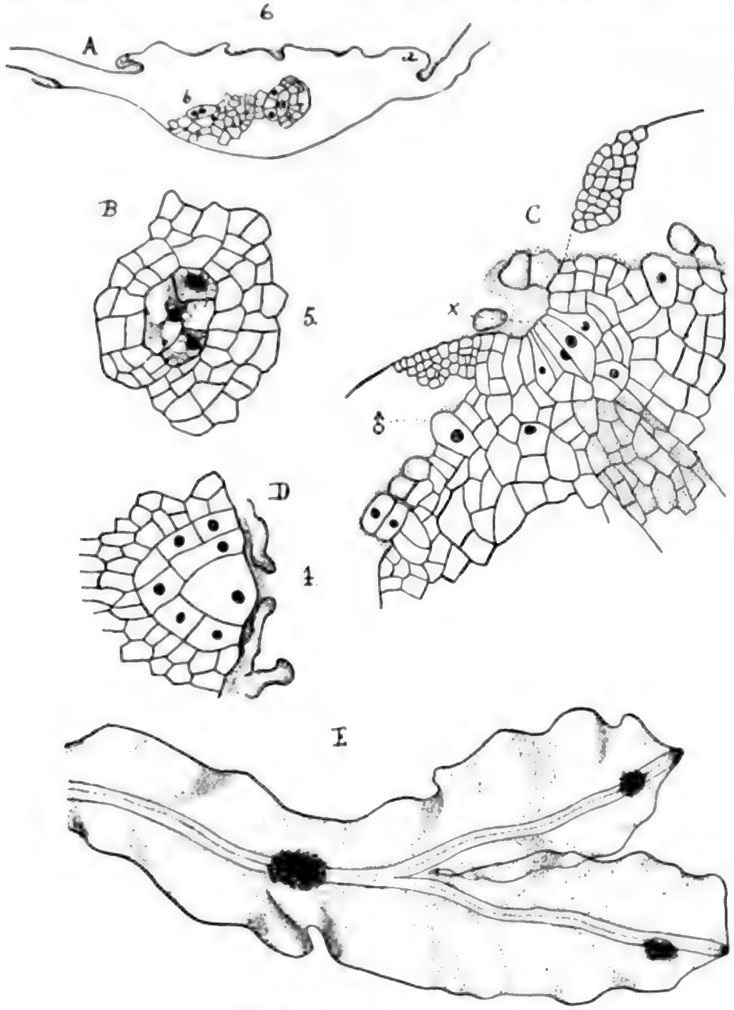

Fig. 8. *Pallavicina radiculosa.*

A. Cross-section of the thallus apex, showing the apical cell, *x*, and the apex, *b*, of a branch. *a*, *a* are the young scales subtending antheridia.
B. The apex of the shoot, more highly magnified.
C. Horizontal section of the shoot apex, showing the apical cell, *x*, and a very young antheridium.
D. Vertical longitudinal section of the apex.
E. Archegonial plant, x 3.

the sides converging somewhat in front. In vertical longitudinal section it appears also triangular, but very much broader (Fig. 8, *D*). A cross-section (Fig. 8, *A*, *B*) shows that the lateral faces meet above and below at an acute angle, so that the whole cell has somewhat the form of a triangular wedge, with the edges directed respectively dorsally and ventrally. The segments cut off from the lateral faces are large, and ordinarily are formed alternately right and left. Before a dichotomy occurs, however, more than one segment may be cut off successively on one side, and one of these presumably gives rise to the apical cell of the new branch, the branching being in the strict sense of the word not a true dichotomy.

In horizontal and vertical longitudinal sections the arrangement of the segments derived from the apical cell is much the same. In cross-section the elongated, almost oval cell appears surrounded by the crescent-shaped segments (Fig. 8, *A*, *B*). Fig. 8, *A* shows a cross-section of the thallus apex shortly after the dichotomy is complete, and the growing point of the new branch is established. The lobes *a*, *a'*, are the beginnings of young antheridial scales, while the group of cells, *b*, is the growing point of the new branch. The divisions of the apical cell are not in quite the same plane as those of the original apex.

Each segment cut off from the apical cell first divides transversely into an adaxial and an abaxial cell. The latter cell divides only by walls perpendicular to the plane of the thallus, and contributes to the wing or lamina of the thallus, which remains permanently but a single cell in thickness. The adaxial cell divides crosswise into a middle and an inner cell. The former forms the outer tissues of the midrib, and also from it arise the antheridia. The innermost cell, by subsequent repeated longitudinal divisions, gives rise to the narrow cells of the conducting strand traversing the midrib. These cells at first have dense contents, which later mostly disappear. A section of the young conducting strand is shown in Fig. 7, *B*.

The entire apex of the shoot, and the younger antheridia, are bathed in mucilage which is secreted by two-celled glandular hairs developed from the outer cells of the young segments; and similar mucilage secreting hairs are also found among the antheridia.

Pallavicinia Levieri Schiffner

Pallavicinia Levieri, the third species considered here, is much less restricted in its distribution. It is quite common in the neighborhood of Tjibodas in Java, at an elevation of 1400-1500 metres, and material was collected at several points. It has been reported from several other sta-

tions in Java and Sumatra, and according to Stephani occurs also in the Pacific Islands, Tahiti and Hawaii. It will probably be found in other parts of Polynesia.

The plant (Fig. 9) is smaller than *P. radiculosa,* and there is much more difference in size between the male and female plants.

Like *P. radiculosa,* the thallus is prostrate. It usually occurs on the trunks of trees, among other liverworts and mosses, and does not form masses of large size. The plants are very delicate in texture, and the male plants are noticeably smaller than the females or the sterile plants. They

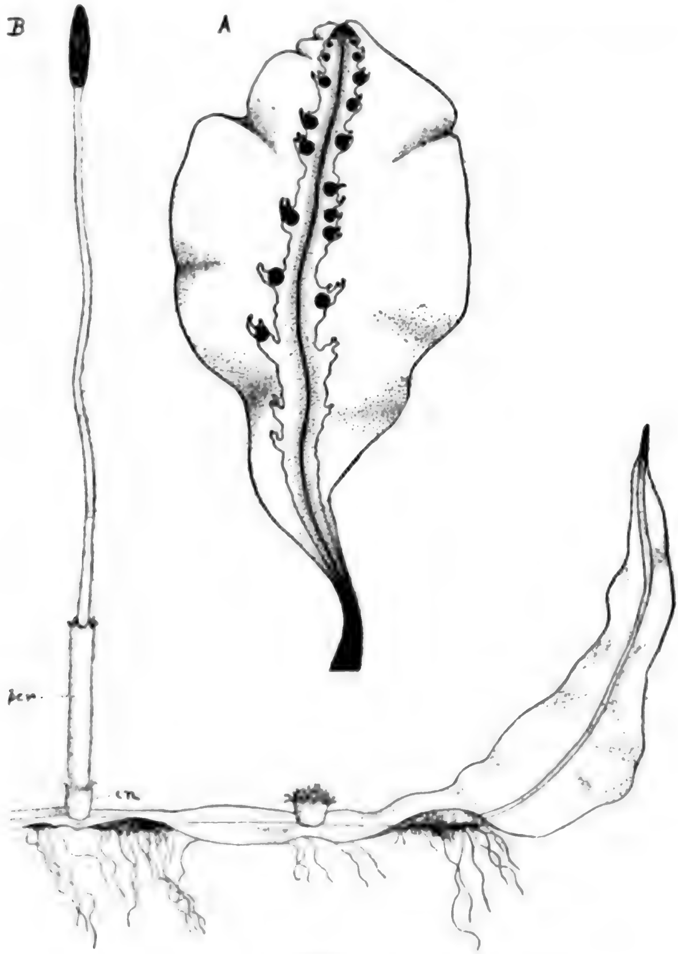

Fig. 9. *Pallavicinia Levieri.*
A. Male plant, x 8. *B.* Female plant, x 4.

measure only about 2 cm. in length and 4-5 mm. in width. The female plants (Fig. 9, *B*) are about 10 cm. in length and 7 mm. wide.

The wings of the thallus are relatively very wide, and as usual but one cell thick. They are waved slightly on the margin, which is entire except for an occasional cell which projects slightly so as to form an inconspicuous tooth. Anteriorly the lamina of the antheridial plant narrows abruptly to the apex of the shoot, which is indented. The midrib projects strongly on the ventral side. The rhizoids are much less numerous than in *P. radiculosa*, and quite different in color, being a rather light brown, instead of the deep purple-red found in *P. radiculosa*. The conducting strand of the midrib is much like that of *P. radiculosa*.

From the sides of the midrib in the male plant extend a series of scales which form a more or less continuous shelf-like structure. These scales have their free margins deeply lobed and toothed, and underneath the shelf formed by these confluent scales the antheridia occur, either singly or in groups of several together (Fig. 9, *A*). The antheridia arise in acropetal succession, and are arranged in a somewhat broken row along each side of the midrib. They are more completely covered by the subtending scales than is the case in *P. radiculosa*, and are not so evidently divided into groups separated by sterile areas.

The antheridia, to judge from a somewhat cursory examination, appear to agree in all essential details of structure with those of *P. radiculosa*.

The apical cell of the thallus is not so deeply placed as in *P. radiculosa*, but a study of horizontal and vertical sections shows that it has the same form. On the ventral surface of the midrib in *P. Levieri*, as in *P. radiculosa*, there may occasionally be found small groups of meristematic cells, which appear dormant, and do not show a definite apical cell. The smaller groups are slightly sunken; the larger ones, perhaps having resumed activity, form hemispherical protuberances. The origin and development of these groups of cells is apparently the same as the similar ones in *P. Zollingeri*, and probably under favorable conditions these give rise to normal branches.

The archegonial plants of *P. Levieri* (Fig. 9, *B*), besides being much larger than the male plants, show also a very different appearance at the apex of the shoot. There is no indentation at this point, but the thallus is prolonged ino a nearly cylindrical process of some length, in which the wings are quite suppressed. It is possible that an examination of a larger number of individuals might show that this difference in apices of the male and female plants is not constant. The rhizoids of the female plants

of *P. Levieri* were much longer than those of either of the other species that were studied, sometimes reaching a length of a centimeter or more The archegonial receptacles are smaller than those of *P. radiculosa*, and are more like those of *P. Zollingeri*.

The Antheridium

Of the three species examined, *P. radiculosa* was the best for the study of the young antheridium, as most of the stages of development were found in the material.

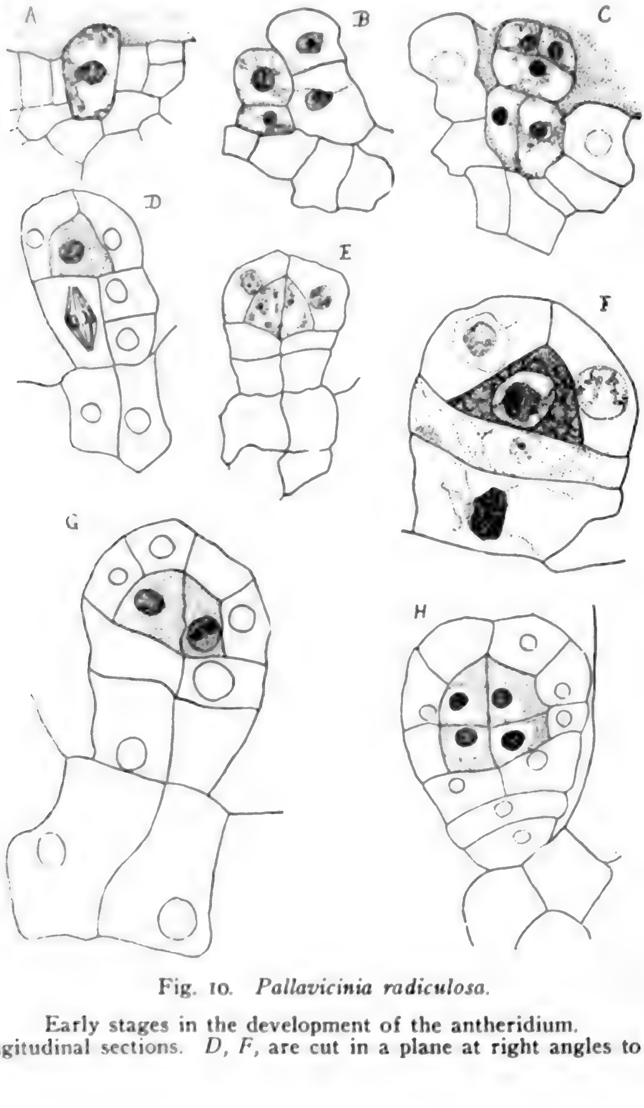

Fig. 10. *Pallavicinia radiculosa.*

Early stages in the development of the antheridium. Longitudinal sections. *D, F*, are cut in a plane at right angles to *E, G*.

The young antheridium arises very near the apex of the thallus, as a single large cell, projecting from the side of the midrib (Fig. 10, *A*). The first division wall is transverse, and separates a basal cell which takes no part in the development of the antheridium itself, and an outer cell, which is the real mother-cell of the antheridium (Fig. 10, *B*). At about the same time that this transverse division is formed in the young antheridium, certain neighboring superficial cells of the midrib become evident, which later form special structures accompanying the antheridia. Some of these "companion cells" secrete the mucilage which bathes the young antheridia; while others, not always readily distinguishable from the earliest stages of the antheridia themselves, finally develop into the characteristic scales covering the older antheridia, somewhat as described by Campbell [1] for Aneura.

The divisions in the antheridium show some variation. Of the two cells formed by the first transverse wall, the inner one divides by a vertical wall into two cells, which remain sunk in the midrib and usually divide no further (Fig. 10, *C-E*), and may usually be recognized at the base of the stalk in the fully developed antheridium.

The first wall in the antheridium itself is also transverse. Of the two cells thus formed, the lower gives rise to the stalk of the antheridium, and also to the layer of cells separating the sperm-cells from the stalk of the antheridium. The outermost of the two original cells divides first by a median vertical wall, and each of these cells is next divided by a nearly periclinal wall into two very unequal cells. This wall intersects both the outside wall of the antheridium and the median wall, and is quickly followed by a second similar wall which meets the first one and also intersects the median wall. A cross-section of the antheridium at this stage (Fig. 11, *A*) shows two triangular central cells surrounded by four narrow peripheral ones. The young antheridium at this stage closely resembles that of *Porella Bolanderi* (Campbell [1], Fig. 52), and differs from the usual type of the Jungermanniales, where, according to Leitgeb ([1], II, p. 44) these two peripheral cells do not extend to the top of the antheridium, and a third peripheral cell is cut off before the separation of the central cell is complete. The appearance of longitudinal sections of the young antheridium, cut respectively in the plane of the first median wall, and at right angles to it, are shown in Fig. 10, *D, G, E, H*. Cross-sections of similar stages are shown in Fig. 11, *A, C*. The next divisions take place in the peripheral cells, and in the stalk, the two primary spermatogenous cells remaining undivided until the stalk is well developed and

the four original peripheral cells of the antheridium have each divided at least once (Fig. 10, *G*). The first division in the central cells is a transverse one, quickly followed by a vertical division, so that whether in longitudinal- or cross-section, the central cells are arranged quadrant-wise (Figs. 10, *H*, 11, *B*). The subsequent divisions follow rapidly, but without any

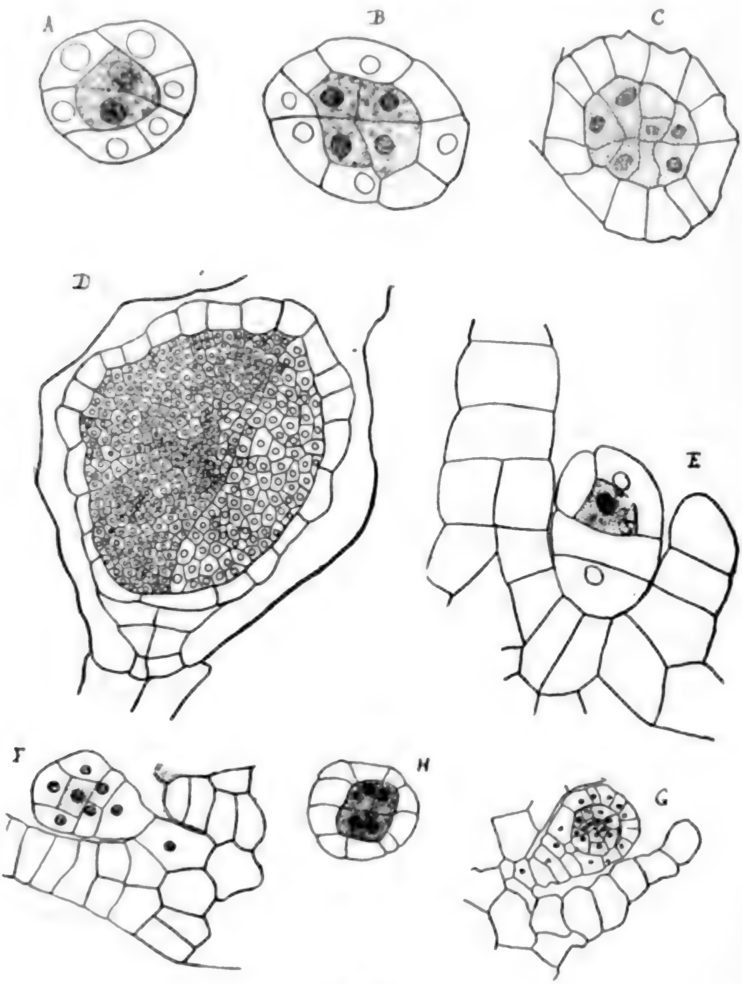

Fig. 11.

A-D. P. radiculosa; E-G, P. Levieri.
A-C. Cross-section of young antheridia.
D. Longitudinal section of a nearly ripe antheridium.
E-G. Longitudinal sections; *H*, transverse section.

definite succession being evident. There is but little displacement of the original division-walls, so that up to the last divison of the sperm-cells the limits of the earlier divisions can be plainly traced, and the spermatocytes are in irregular blocks marking the early divisions. While within these blocks of cells the nuclei are usually in the same stage of mitosis, each segment of the antheridium may show a different stage of nuclear division. This was also noted by Humphrey in his study of *Fossombronia longiseta* [1].

Spermatogenesis

Pallavicinia Zollingeri proved the best species for a study of spermatogenesis, and the investigation of this subject was mainly devoted to that species. In the earliest stages procurable the final mitosis had taken place, and the two resulting nuclei had begun to assume the elongated form found in the completed spermatozoid (Fig. 12, *A, B*). The final mitosis is accompanied by the formation of a delicate but perfectly evident division wall separating the pair of spermatocytes. The spermatocytes at this stage closely resemble those of *Calycularia radiculosa* (Campbell [2], Fig. 7). The length of the young spermatocyte in *P. Zollingeri* is about 7μ. Fig. 12, *A*, shows the pair of spermatocytes at this stage. The blepharoplast (*bl.*) now has the form of a somewhat curved rod at the end of the elongated nucleus. Sometimes the blepharoplasts of the pair of spermatocytes are at the same end, sometimes at opposite ends. With the development of the spermatozoid, the blepharoplast, as usual, elongates rapidly, and becomes a slender curved rod, hooked at the free apex, and following the curve of the elongating nucleus which becomes crescent-shaped, with the anterior end more or less conspicuously attenuated (Fig. 12, *D-K*). In some of the preparations there was present between the blepharoplast and the anterior part of the sperm-nucleus a thick, rod-shaped body, which perhaps represents the "Nebenkörper" described by Ikeno [1] in Marchantia. The cilia arise from the blepharoplast a short distance back of the apex, and become finally about as long as the body of the free spermatozoid, which is about 16μ in length.

The development of the spermatozoid in *P. radiculosa* was found to be so much like that of *P. Zollingeri* that no attempt was made to follow it in detail. However, some of the later stages in the last mitosis of the spermatocyte, which were not seen in *P. Zollingeri*, were secured in *P. radiculosa*. The nuclei are so small that difficulty was experienced in determining the number of chromosomes, which is probably eight (see Fig. 12, *N-Q*). The spermatocytes are separated, as in *P. Zollingeri*, by a delicate membrane, which is more difficult to demonstrate

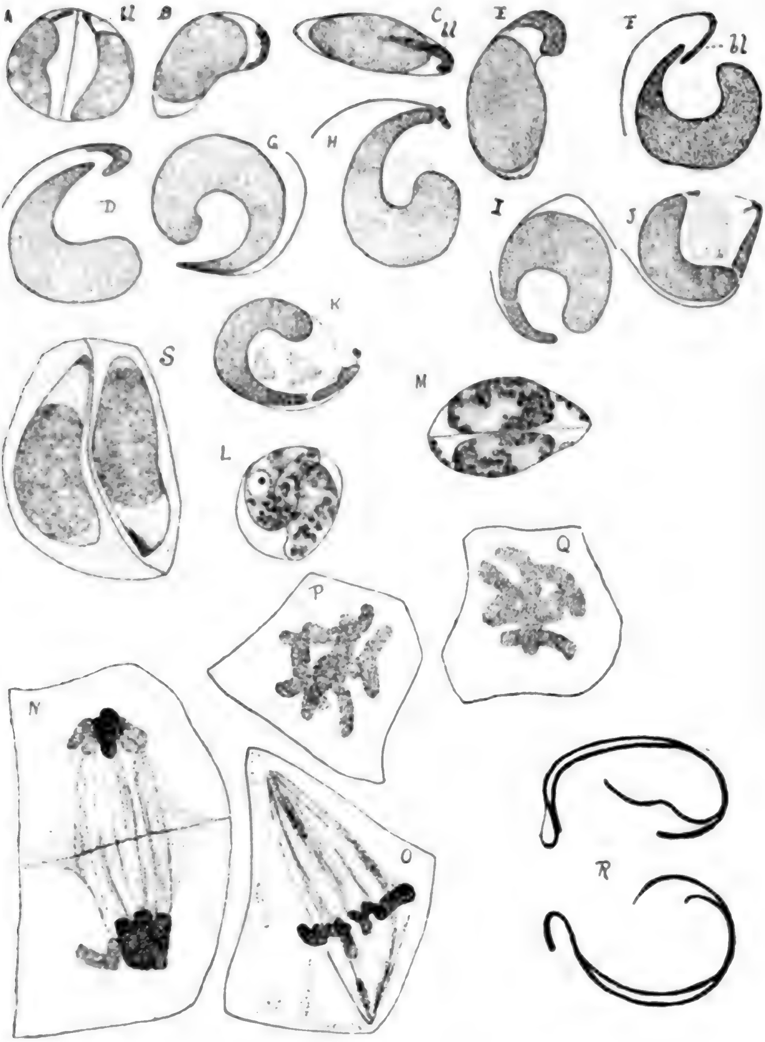

Fig. 12.

A-M. Spermatogenesis in *Pallavicinia Zollingeri*.
L. Pair of spermatocytes seen from above.
M. Similar spermatocytes seen in profile.
N, O. Last mitosis in the spermatocytes of *Pallavicinia radiculosa*.
P-Q. Polar view.
R. Spermatozoids of *P. Zollingeri*.
S. Pair of spermatocytes of *P. Levieri*.
All magnified about 2,000 times.

than in that species. The best differentiation was secured by Haidenhain's iron-alum-haematoxylin. The blepharoplasts could not be made out, but presumably are present.

A sufficient study of the spermatogenesis in *P. Levieri* was made to show that it is very much like that in the other two species. Fig. 12, *S*, shows the pair of spermatocytes with the separating membrane and the blepharoplasts. The spermatocytes are somewhat larger than corresponding stages in *P. Zollingeri*, measuring about 9μ in length.

The Archegonium

In all species of Pallavicinia the archegonia are in groups surrounded, as already stated, by a double envelope: an outer one, the involucre, much the more conspicuous before the fertilization of an archegonium; and an inner one, which is very small at first, but which after an embryo is formed grows rapidly and forms a conspicuous tubular sheath enclosing the developing sporophyte.

In *P. Zollingeri*, the involucre is cup-shaped, with a lobed margin (Fig. 6, *G*, *H*). Within this, and surrounding the base of the archegonial group, is the young perianth, which at this stage does not reach above the level of the venter of the archegonia (Fig. 13). *P. radiculosa* (Fig. 13, *A*, *B*, *E*) differs from *P. Zollingeri* mainly in the much greater number of archegonia in the receptacle, and in the more flaring and deeply fringed involucre. *P. Levieri* is somewhat intermediate in character, both as to the number of archegonia and the form of the involucre (Fig. 13, *D*).

The receptacle is at first level with the surface of the thallus, but as new archegonia develop it becomes raised and forms a more or less prominent elevation, or placenta, to which the archegonia are attached (Fig. 13, *E*).

Of the three species examined, *P. radiculosa* was the best for the study of the archegonium, as all stages of development were present in the material. *P. Levieri* also showed most of the stages, but as it differed very little from *P. radiculosa* an exhaustive study was not made. None of the specimens of *P. Zollingeri* showed very young archegonia, but to judge from the few immature archegonia that were seen it does not differ essentially from the other species.

Pallavicinia radiculosa, while agreeing in the main with other anacrogynous Jungermanniales, in the development of the archegonium shows certain differences that may be noted.

The youngest archegonia (Fig. 14, *A*, *C*) show a stalk composed of two or three cells, and a terminal, approximately hemispherical cell from

which the archegonium itself is developed. In this terminal cell, as in all Hepaticae, three nearly vertical, intersecting walls are formed, surrounding an axial cell. In longitudinal sections two of the peripheral cells are seen, with the axial cell between (*B, C*); in cross-section, the axial cell appears triangular in shape (*F*).

The young archegonium as it grows in length becomes divided into two stories, by a transverse wall in each cell, and this first transverse division separates the basal part, or venter, from the neck. In the three peripheral cells, or more commonly in only two of them, a longitudinal division is formed, so that the axial cell is surrounded by five rows of peripheral ones. In the ventral region, other longitudinal walls are formed subsequently, but in the neck region no further longitudinal divisions occur, and a cross-section of the neck shows a central cell surrounded by

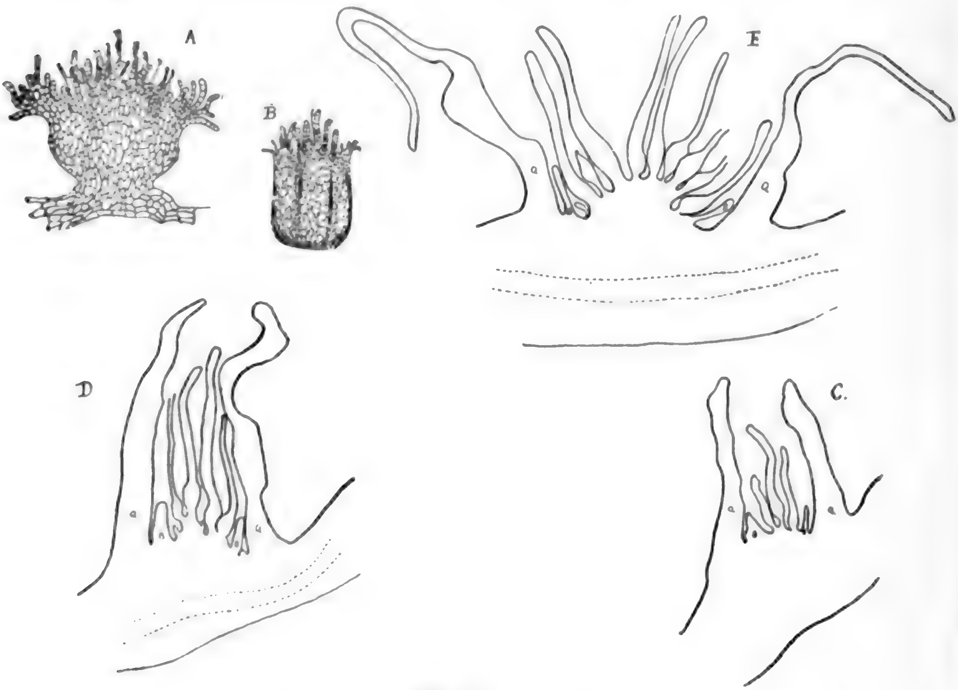

Fig. 13.

A. Archegonial receptable of *P. radiculosa*.
B. The same with the involucre removed.
C. Section of the receptacle of *P. Zollingeri*.
D. Section of the receptacle of *P. Levieri*.
E. Section of the receptacle of P. *radiculosa*.
a. Involucre; *b*, perianth.

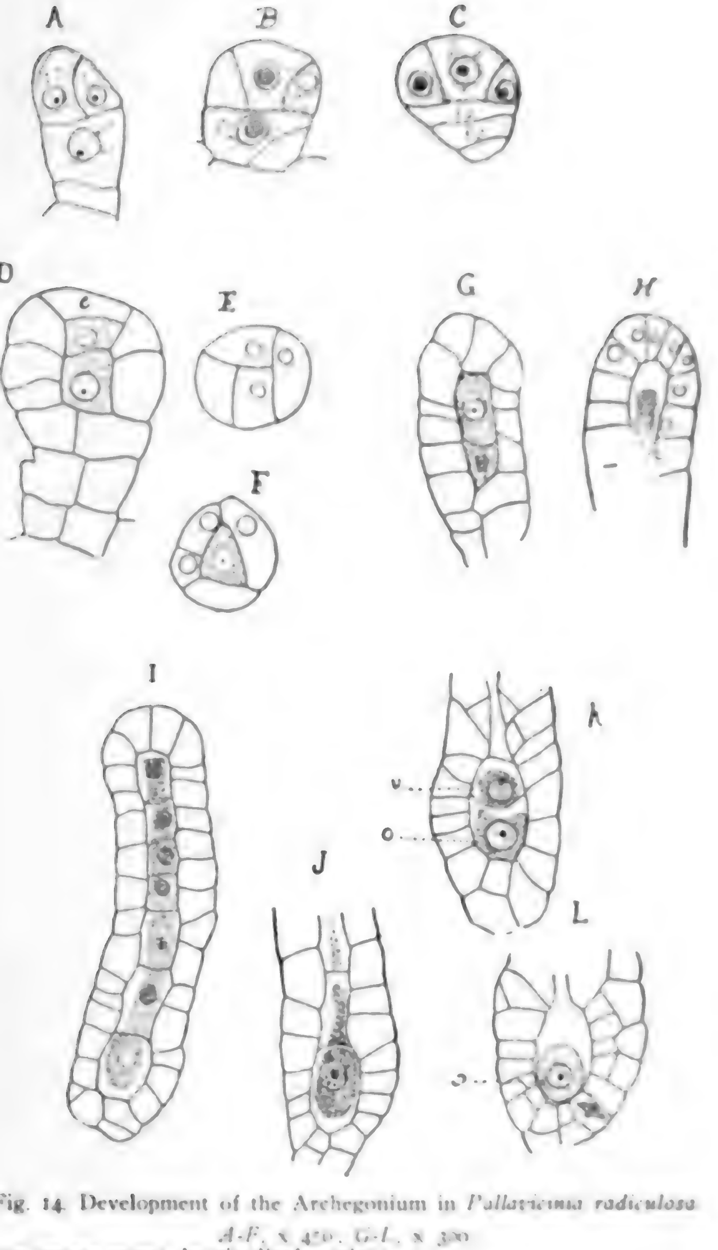

Fig. 14. Development of the Archegonium in *Pallavicinia radiculosa*.

A-F, × 450; *G-L*, × 300.

A-C. Very young stages, longitudinal sections.
D. A somewhat older one; the cap-cell, *c*, is still undivided.
E. Cross-section of the apex of a somewhat older stage; the divisions are somewhat irregular.
F. Cross-section of a very young archegonium.
G. An older stage.
H. Apex of a still older archegonium, showing a certain amount of apical growth.
I-L. Older stages. *v*, ventral canal-cell; *o*, egg-cell.

five peripheral ones. Occasionally, as in the Marchantiales, there are six peripheral cells, but this is not usual.

The axial cell divides first by a transverse wall, and from the ventral cell arises by a subsequent division, the egg-cell, and the ventrai canal cell (Fig. 14, *K*). The upper of the two original axial cells next has cut off from it a terminal, or cap-cell (Fig. 14, *D*). This cell may divide almost at once by two intersecting walls, into four cells arranged quadrant-wise when seen in cross-section; but in *P. radiculosa* this quadrant division is not always evident, and the cap-cell undergoes a considerable number of divisions which add to the upper part of the neck (Fig. 14, *G*, *H*). There is thus a limited apical growth of the neck, as well as growth due to intercalary divisions of the original neck-cells. This apical growth suggests that found in the moss-archegonium, but is much less prominent, and does not give rise to any of the canal-cells, which are all derived by division from the original neck canal-cell.

Gayet [1] states that he found a similar apical growth in a large number of liverworts, but his statements have not been confirmed by subsequent investigations. (See Campbell [1].)

The original neck canal-cell gives rise to five or six in the mature archegonium (Fig. 14, *I*). The neck may become very much elongated (Fig. 15), a single row of the outer cells containing as many as forty cells. The neck, in these elongated archegonia, usually becomes twisted.

Up to the time of the separation of the egg-cell and ventral canal-cell, the outer part of the venter consists only of a single layer of cells (Fig. 14, *I*, *J*); but it later becomes divided into two layers by a series of periclinal divisions (Fig. 14, *L*).

P. Levieri differs mainly from *P. radiculosa* in the earlier separation of the cap-cell, and the regular division of this into quadrants, so that usually the cap-cell does not contribute to the growth in length of the archegonium-neck (Fig. 15, *C-E*).

The archegonia of *P. radiculosa* are larger than those of *P. Zollingeri*, and the periclinal walls in the venter seem to be formed at a rather earlier stage. *P. Levieri* resembles *P. radiculosa* in the size and form of the archegonium, but the involucre itself is more like that of *P. Zollingeri*.

After fertilization the egg develops into the embryo, about which is developed the calyptra, formed from the much enlarged venter of the archegonium. The neck of the archegonium is carried up and forms a slender process tipping the massive cylindrical calyptra. The latter is not formed exclusively of the enlarged archegonium venter, but the adjacent tissue also contributes to it. When complete the calyptra forms a sheath

five to ten cells in thickness, enclosing the young sporophyte. With the growth of the calyptra the unfertilized archegonia are carried up, sometimes appearing almost at the summit (Fig. 22, *A*). These sterile archegonia may become much elongated and their necks twisted.

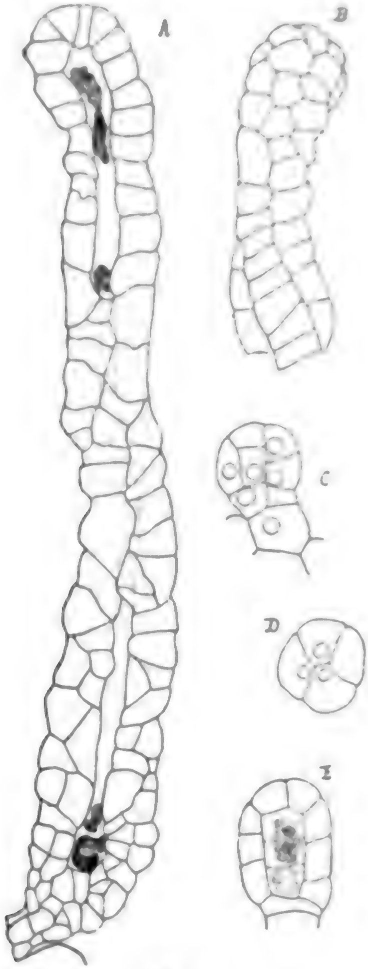

Fig. 15.

A. An old archegonium of *Pallavicinia radiculosa*, with much elongated neck.
B. Surface of the upper part of a similar archegonium, showing the twisting of the neck.
C. Young archegonium of *P. Lyellii*, x 300.
D. Apex of a somewhat older one, showing quadrant arrangement of the four terminal cells.
E. Young archegonium of the same species.

The Embryo

The only account of the development of the sporophyte in the genus Pallavicinia that we have been able to find is that of *P. decipiens*. In this species Farmer [1] gives a brief description and figures of early stages of the embryo, which seems to differ a good deal from that of *P. Zollingeri* and *P. radiculosa*, and to more nearly resemble that of *Mörkia hibernica*. (See Leitgeb [1], Pt. III, Pl. vi.)

While the sections of the embryos that were obtained were more or less badly shrunken, still the most important points in their development could be made out pretty well. Most of the younger stages found were of *P. Zollingeri*, but a few were also found in *P. radiculosa* and *P. Levieri* which agreed closely with the former species.

The youngest specimen that was examined consisted of two nearly equal cells, separated by a transverse wall (Fig. 16, *A*). The next division probably is also transverse, and arises in the upper cell, dividing the embryo into three superimposed cells, as is the case in *P. decipiens*. In the next older stage that was found, the embryo showed two large basal

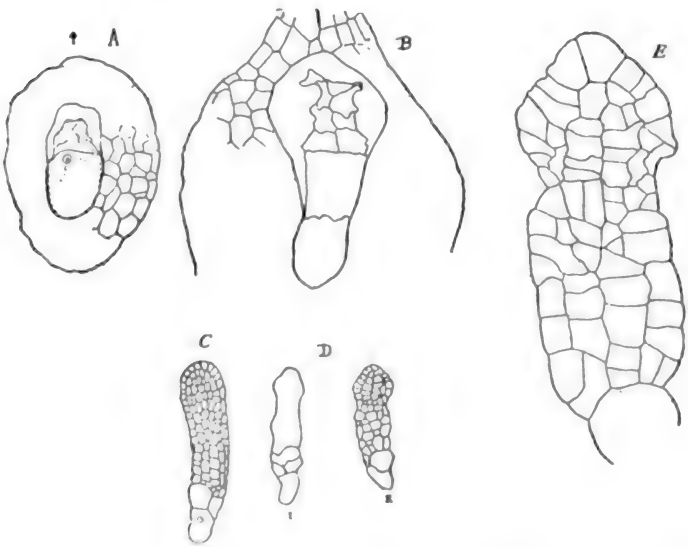

Fig. 16. *Pallavicinia Zollingeri.*

A. Two-celled embryo, enclosed in calyptra, x 200.
B. An older embryo.
C, D. Older embryos, x about 50.
E. Upper part of *D*, more highly magnified.

cells, forming a sort of suspensor, and a terminal portion, consisting of four tiers of cells, from which all of the sporogonium except the suspensor is derived (Fig. 16, *B*). It is probable that two of the three primary cells of the embryo contribute to the suspensor, while all the rest of the sporophyte—foot, seta and capsule—is derived from the terminal cell. This, however, was not positively demonstrated.

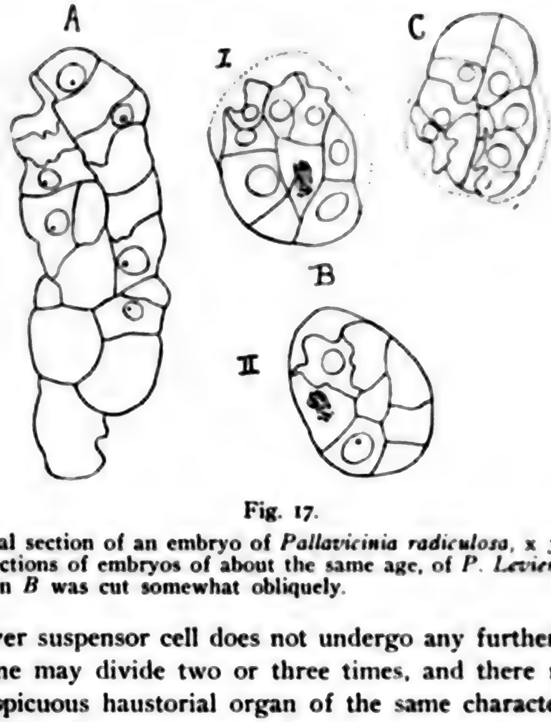

Fig. 17.

A. Longitudinal section of an embryo of *Pallavicinia radiculosa*, x 300.
B, *C*. Cross-sections of embryos of about the same age, of *P. Levieri*. The embryo shown in *B* was cut somewhat obliquely.

The lower suspensor cell does not undergo any further division, but the upper one may divide two or three times, and there results an extremely conspicuous haustorial organ of the same character as that observed in various Jungermanniales, both acrogynous forms like ***Jungermannia bicuspidata*** and anacrogynous types like Aneura. (See Leitgeb [1], Clapp [1].)

Material was wanting for the next stages of development, but to judge from such stages as those shown in Fig. 16, *C-E*, the first division in the terminal cell of the embryo is vertical, and this is followed later by a series of transverse divisions. There is, however, a certain degree of irregularity in the divisions, as there is considerable variation in the arrangement of the cells in different embryos.

The upper part of the embryo rapidly elongates, and forms a nearly cylindrical body, the apex of which is slightly enlarged, and marks the

beginning of the capsule, or sporogenous region. It was not possible to determine the relation of the three regions of the young sporophyte, *i. e.*, capsule, seta, and foot, to the early divisions in the terminal cell of the embryo.

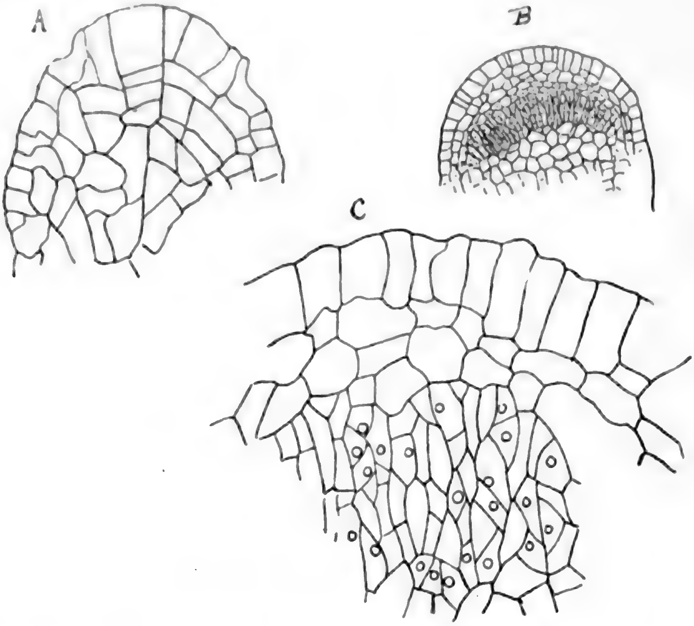

Fig. 18. *Pallavicinia Zollingeri.*

A. Upper part of a young sporophyte, x 300.
B. Upper part of an older sporophyte, showing the sporogenous tissue; x about 60.
C. Portion of *B*, more highly magnified.

In *P. decipiens* the young embryo is much shorter than in either *P. Zollingeri* or *P. radiculosa*, and more nearly resembles that of Mörkia, although more elongated than in the latter. Like Mörkia, also, the suspensor is much less conspicuous than in either *P. Zollingeri* or *P. radiculosa*.

The first periclinial walls in the terminal portion of the embryo probably determine the separation of the sporogenous tissue from the wall of the capsule (Fig. 16, *E*). The foot is much less clearly marked than in Mörkia, but is more evident in *P. Zollingeri* than it is in *P. radiculosa;* nor is the delimitation of the capsule and seta as definite as in either *P. decipiens* or Mörkia.

Of the three species examined, *P. Zollingeri* most nearly resembles

Mörkia in the character of the foot, which is somewhat bulbous, while in *P. radiculosa* the foot is pointed and merges more or less gradually into the seta. *P. Levieri* is somewhat intermediate between *P. Zollingeri* and *P. radiculosa* in the form of the foot.

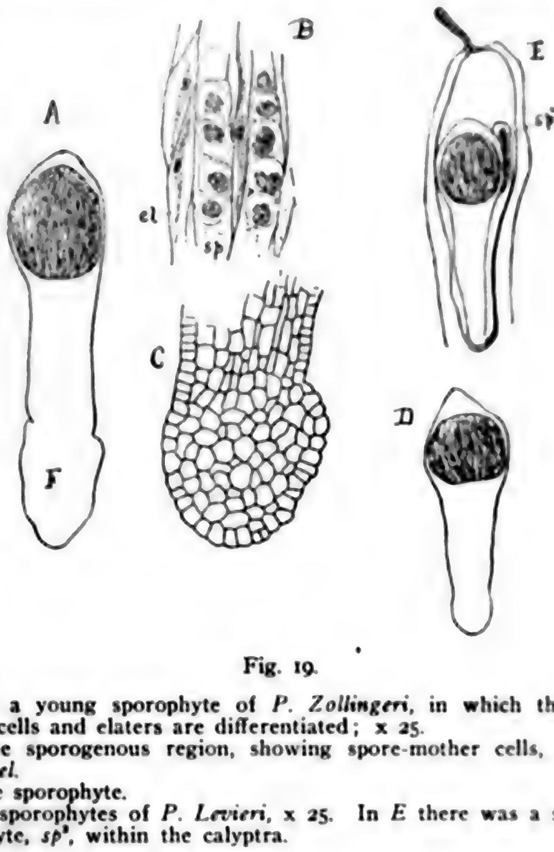

Fig. 19.

A. Section of a young sporophyte of *P. Zollingeri*, in which the young spore mother-cells and elaters are differentiated; x 25.
B. Part of the sporogenous region, showing spore-mother cells, *sp*, and young elaters, *el*.
C. Foot of the sporophyte.
D, E. Young sporophytes of *P. Levieri*, x 25. In *E* there was a second abortive sporophyte, *sp'*, within the calyptra.

As the capsule develops the wall becomes clearly delimited from the sporogenous tissue within. The wall is composed of about three layers of cells throughout most of its extent. In *P. Zollingeri* (Fig. 18, *C*) the wall is three-layered also, or sometimes four-layered at the apex, the outer layer having the cells conspicuously larger than the two inner layers. In *P. radiculosa* (Fig. 21, *A*) the wall at the apex of the capsule is much thicker, and forms a conspicuous beak. *P. Levieri* is intermediate in this respect also between *P. Zollingeri* and *P. radiculosa*.

The sporogenous tissue in *P. Zollingeri* forms at first a somewhat

convex disk, which in section (Fig. 18, *B*) appears as a broad band of narrow cells in vertical rows. Some of these cease to divide, and later become much elongated, giving rise to the elaters; while the others, dividing by transverse walls into rows of isodiametric cells, become the mother cells of the spores. In *P. radiculosa* the sporogenous region, even at first, is more extensive than in *P. Zollingeri*.

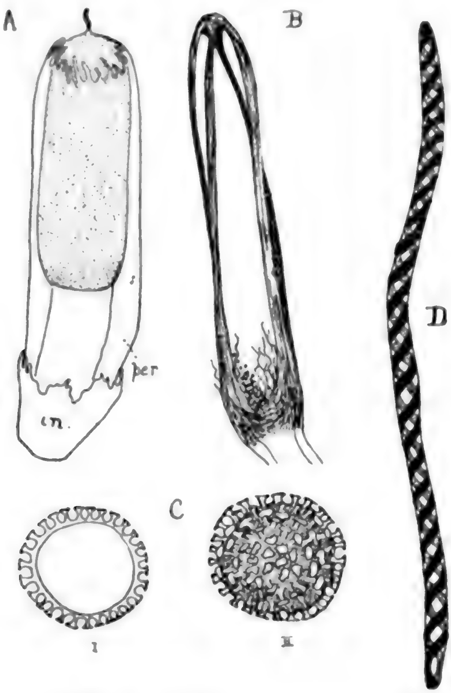

Fig. 20. *Pallavicinia Zollingeri.*

A. Young sporophyte still enclosed in the calyptra. *in*, involucre; *per*, perianth.
B. Open capsule, showing the four coherent valves.
C. I, section; II, surface view of ripe spores.
D. Elater.

By the time that the perianth is fully developed the sporophyte, closely invested by the calyptra, reaches about half-way to the top, and the separation of the sporogenous tissue into the spore mother-cells and elaters is plainly evident (Fig. 19, *A*, *B*). By the time that the sporophyte emerges from the perianth the spores have passed the final stage of division and are nearly mature. The material of *P. Zollingeri* did not furnish preparations showing the details of mitosis in the final stages

of spore-division. Farmer [1] has given a full description of the nuclear division in the spore mother-cells of *P. decipiens*, where he describes a quadripolar spindle. A similar condition has been noted in *Calycularia radiculosa* (Campbell [2]); but in *Pallavicinia radiculosa* (Fig. 21) and *P. Levieri*, which were the only species in which division-stages were encountered, there was no certain evidence of the formation of a quadripolar spindle. As usual in the Jungermanniales, the spore mother-cells are deeply four-lobed.

The full-grown sporophyte in *P. Zollingeri* is about 3.5 cm. in height,

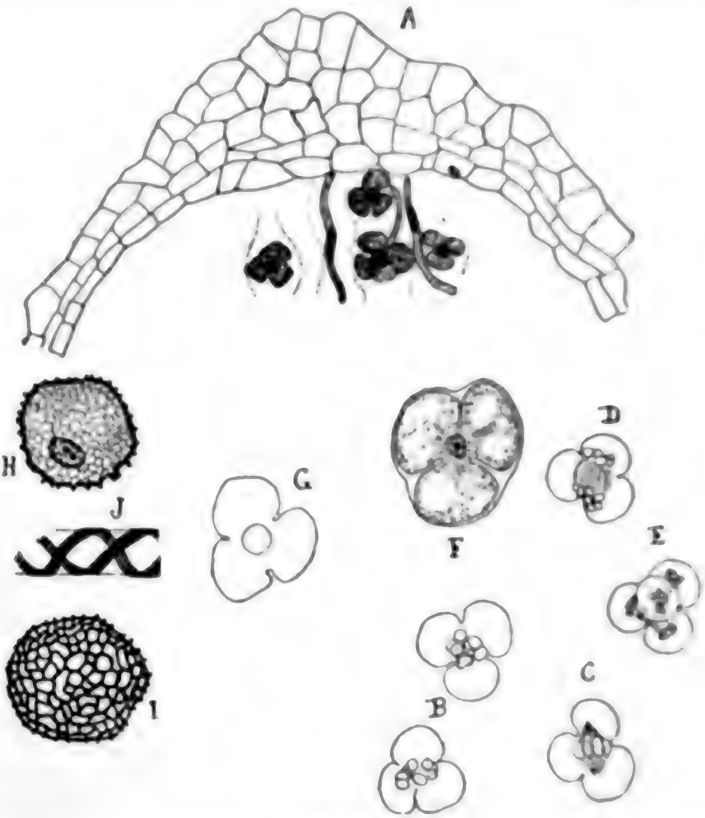

Fig. 21.

A. Upper part of the capsule of *Pallavicinia radiculosa*, showing first stages of division in the spore mother-cells.
B-E. Stages in the mitosis of the spore mother-cells in *P. radiculosa*, x 640.
F. Spore mother-cell of *P. Zollingeri*, x 640.
G. Spore mother-cell of *P. Levieri*, x 640.
H-J. Ripe spores and part of an elater of *P. radiculosa*.

the capsule, which is elongated oval in outline, being about 4 mm. in length by 1.5 mm. in breadth. The ripe capsule opens by four longitudinal slits, but the apical cap remains entire, so that the four valves between the slits remain together at the apex (Fig. 20, *B*). The ripe spores (Fig. 20, *C*) measure about 14μ in diameter, and the outer surface is covered with closely set blunt papillae, with somewhat expanded outer

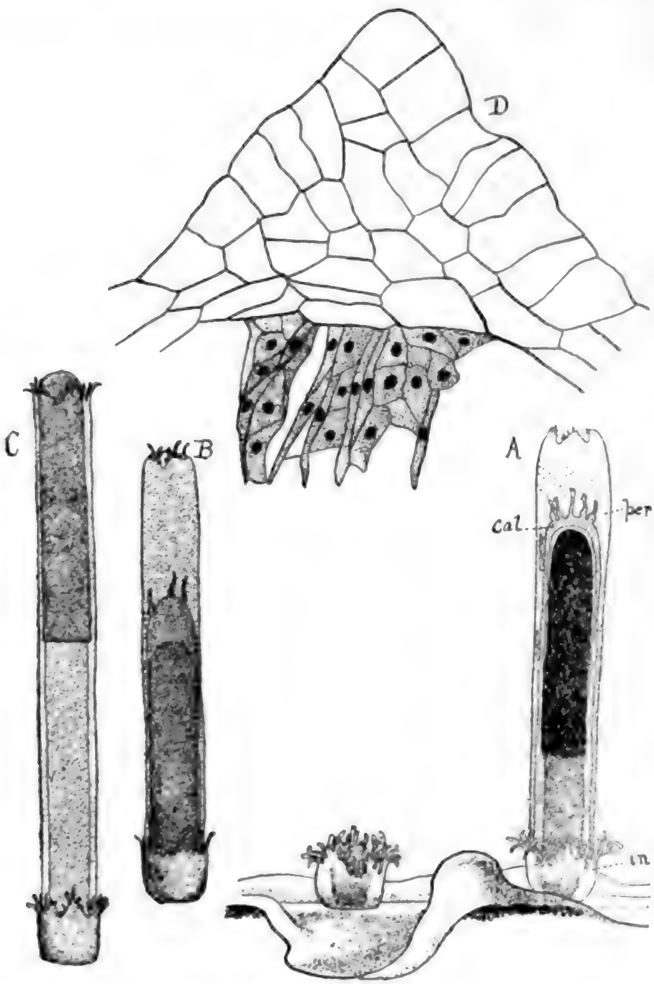

Fig. 22. *Pallavicinia Levieri.*

A-C. Young sporophytes. *A* and *B* still included within the calyptra; *C*, after breaking through.
D. Section of upper part of the capsule, highly magnified.

ends. The elaters have two spiral bands. The one figured, which measured 150μ in length, was somewhat shorter than the majority of them.

The mature sporophyte of *P. radiculosa* differs from that of *P. Zollingeri* in its shorter seta, which, according to Schiffner [1], is only 15-20 mm. in length. The capsule, however, is much longer than in *P. Zollingeri*, but almost perfectly cylindrical in form, scarcely exceeding in width the seta (Fig. 23, *D*). As already stated, also, the apex is conspicuously pointed. It opens in the same way, by four narrow valves, united at the apex. Except at the pointed apex, the wall of the capsule is composed of three layers of cells, of which the outer one has the cell-walls uniformly thickened, and dark colored. The markings on the ripe spores form a network of delicate ridges, much like those in Fossombronia, but quite different from those found in *Pallavicinia Zollingeri* (Fig. 21, *I*, *J*). The ripe spores are 12-15μ in diameter, and the elaters often measure about 225μ in length.

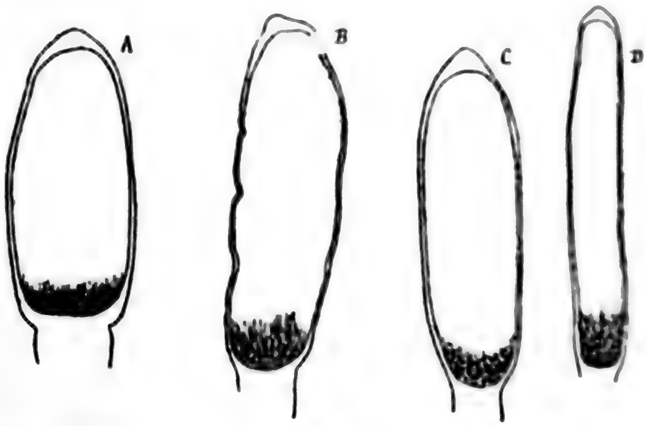

Fig. 23.

Sections of the capsules of *P. Zollingeri*, *A*; *P. Levieri*, *B*; *P. indica*, *C*; *P. radiculosa*, *D*. *B* and *D* are not fully grown.
A-C, x 18; *D*, x 10.

Spore Division

Long before any sign of the final nuclear division in the spore-mother-cell can be seen the cell becomes deeply four-lobed, as in all Jungermanniales. The mother cell in *P. Zollingeri* (Fig. 21, *L*), is decidedly larger than in *P. radiculosa*, but its nucleus is smaller. Traces of what looked like the quadripolar spindle described by Farmer in *P.*

decipiens could be sometimes seen, and at the extremity of the rays of the spindle was a body which may have been a centrosphere. The material, however, was not very well stained, and the nature of these bodies was not perfectly clear. As no stages of mitosis were seen, it remains to be seen whether the chrmosomes are four in number, as in *P. decipiens* (Farmer [1]), or eight, as in *P. radiculosa*.

In the latter species (Fig. 21, *A*, *E*), there are eight chromosomes,—thick, somewhat kidney-shaped bodies; and instead of the quadripolar spindle there is a conspicuous bipolar spindle of the usual form. The chromosomes divide and arrange themselves in two groups which move to the poles of the spindle, where without assuming the form of a resting nucleus they divide again, and a second bipolar spindle is formed. It was supposed that as the result of a reduction division there would be only four chromosomes in the young spores; but there is no question that eight are present in most cases, at least, and none were seen where the number was four. A similar condition was found by Farmer in *P. decipiens*, and it is also the case in *Calycularia radiculosa*. (See Campbell [2].)

It still remains to be seen where the reduction division occurs in these liverworts.

SUMMARY

1. The thallus in the two sections of the genus Pallavicinia differs in two respects. In the section Eupallavicinia, the wings are but one cell thick throughout, while in Mittenia the midrib merges gradually into the wings, as is the case in Mörkia and Calycularia. In Mittenia also, there is a marked difference between the prostrate, rhizome-like portion of the thallus and the upright fan-shaped green branches. In the latter also, the formation of adventitious branches from the rhizome is more common than in the species of Eupallavicinia.

2. The apical cell in the three species considered in this paper is a two-sided one, like that of Aneura or Metzgeria. These species differ in this respect from *P. decipiens*, where the apical cell is a three-sided prism (Farmer [1]). *Pallavicinia cylindrica* (Campbell [1]), may have a two-sided apical cell, but more commonly it appears oblong when seen in horizontal section. P. (Blyttia) Lyellii, according to Leitgeb [1], has a two-sided apical cell.

3. The hooked marginal teeth, found in Mittenia, are probably comparable to the leaf-like lobes of certain species of Symphyogyna, and like them bear a definite relation to the segments of the apical cell.

4. The position of the antheridia in the three species studied differs somewhat from the descriptions given by Schiffner [2]. In *P.* (*Mittenia*) *Zollingeri* they cover the whole surface of the midrib, as they do in Mörkia. In the related species, *P. decipiens*, they are said by Farmer [1] to form a row on each side of the midrib. In *P. Levieri* they occur in a row on each side of the midrib, and not on its upper side. In *P. radiculosa* the presence of sterile areas between the groups of antheridia seems to have been overlooked by previous students of this species.

5. The development of the antheridium is much alike in all the species, and conforms to the usual type found in the Jungermanniales.

6. The spermatogenesis corresponds to that found in other Hepaticae. A delicate membrane separates the pairs of spermatocytes, as in Fossombronia and Calycularia. It is possible that a "Nebenkörper," like that described for Marchantia (Ikeno [1]) and for Fossombronia (Humphrey [1]) may be present, but this was not certainly demonstrated. Woodburn [1] believes that such a body is not present in the spermatozoid. The number of chromosomes is probably eight.

7. Of the three species examined, *P. Zollingeri* has the smallest archegonial receptacle, and *P. radiculosa* the largest. The archegonium of *P. radiculosa* shows a limited apical growth due to the activity of the cover-cells.

8. The embryo of Pallavicinia agrees in many ways with that of other Anacrogynae that have been studied. It is perhaps most like that of Aneura in the development of a very large haustaurial organ, or suspensor. In this respect the species under consideration seem to differ a good deal from *P. decipiens*, and from Mörkia. Of the three species, *P. Zollingeri* is nearest to Mörkia in the form of the capsule and the larger foot.

9. The species all agree in the structure of the capsule, which has a more or less conspicuous terminal beak or pad, which remains intact, so that the four valves of the open sporogonium remain attached to each other at the apex, and the capsule opens by four longitudinal slits. The beak is best developed in *P. radiculosa,* which has a much more elongated capsule than the other species. In its much shorter and relatively broader capsule, *P. Zollingeri* is more like Mörkia or Calycularia. *P. Zollingeri* is also like the latter in the tuberculate spores. In *P. radiculosa* and *P. Levieri* the spores are reticulately marked.

CONCLUSION

To judge from the foregoing study of Pallavicinia, *P. Zollingeri* is in some respects more like Mörkia than it is like the other species of Pallavicinia that were examined. This is true of the thallus, which has a broad, indefinite midrib, merging gradually into the wings, instead of the sharply defined midrib, and thin wings of Eupallavicinia. The conducting tissue, however, is well developed. The sporophyte, also, approaches in form that of Mörkia. Whether these differences, combined with the very different habit, are sufficient to warrant the retention of the generic name Mittenia for the dendroid species of Pallavicinia, may be questioned; but on the whole we are inclined to think this is justified and the members of the section Eupallavicinia might properly be transferred to Blyttia.

The inter-relationships of the Jungermanniales are very perplexing. Cavers [2] in his recent excellent summary of the subject points out that there is practically no constant point of difference between the two families Blyttiaceae and Aneuraceae (Schiffner's families Metzgerioideae and Leptotheceae). Cavers places in the first family the genera Blyttia (Pallavicinia), Mörkia, Symphyogyna and Makinoa. In the latter are also included four genera, Aneura, Metzgeria, Umbraculum and Podomitrium. The two latter are often united into a single genus, Hymenophyton, but they are abundantly distinct and probably not closely related. Umbraculum is undoubtedly related to Metzgeria, but Podomitrium, except for the position of the reproductive organs, is hardly distinguishable from Blyttia, either in the structure of the thallus or that of the sporophyte. *P. malaccense*, for example, a species common in Western Borneo, is absolutely indistinguishable from a typical Blyttia, except for the position of the reproductive organs upon short ventral branches, instead of upon the ordinary shoots. We believe that Podomitrium should be placed in the Blyttiaceae, rather than in the Aneuraceae, supposing it seems best to retain these two families, and not unite them into a single one as Cavers suggests.

The production of the reproductive organs upon special branches, which appears to be the only constant difference between the Aneuraceae and Blyttiaceae, seems hardly of sufficient importance to warrant the establishment of two families, especially as, except for the small size of the fertile branches, they do not differ essentially from the ordinary shoots upon which the reproductive organs occur in the Blyttiaceae.

Among the genera about which there has been some controversy is Calycularia. *C. radiculosa*, an interesting species of the Malayan region, was recently studied (Campbell [2]), and it was demonstrated that it has much in common with Blyttia and Mörkia, with which it is doubtless related. Schiffner [3] even thinks it should be transferred to the genus Mörkia and entirely separated from the other members of the genus Calycularia.

While it is still too soon to propose a definitive classification of the thallose Jungermanniales, it may be said that so far as the two families Aneuraceae and Blyttiaceae are concerned, the differences between them are not of sufficient importance to warrant the establishment of two families.

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